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The morphology of cardiac and pyloric foregut of *Aegla platensis* Schmitt (Crustacea: Anomura: Aeglidae)

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Abstract

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The aeglid crab, *Aegla platensis* Schmitt 1942, is endemic to fresh waters in temperate and subtropical regions of South America. The cardiac and pyloric foregut of southern Brazilian specimens of *A. platensis* were fixed in buffered 10% formalin and prepared for scanning electron microscopy. In the cardiac foregut, the gastric mill, lateral wall and cardiac-pyloric valve ossicles were identified, while in the pyloric foregut, dorsally, ventrally and laterally supported ossicles were characterised. These results show the complexity of the *A. platensis* foregut and support the hypothesis that the most complex gastric mills are found in the Brachyura and Anomura.

Keywords

Crustacea, Anomura, Aeglidae, foregut, morphology

Introduction

Aeglid crabs are the only anomurans that occur on the surface and underground in the fresh waters of subtropical and temperate South America (Bond-Buckup and Buckup, 1994).

Morphological studies of the internal organization of the foreguts of decapod crustaceans can reveal their feeding habits (Kunze and Anderson, 1979; Ngoc-Ho, 1984). Huang et al. (1998) analysed the distribution and taxonomy of two closely related species of genus *Ocypode* (Crustacea, Brachyura), concluding that these species could be differentiated not only in various external characters, but also by the structure of their foreguts. They suggested that the structure of the gastric mill could be used as an additional character to define genera and families.

Information on the structure of the decapod foregut can be interpreted phylogenetically and it has been argued that the structural complexity of the gastric mill reflects the evolutionary relationships between decapods, with diet and size acting as modifying factors (Dall and Mortiary, 1983). In a cladistic study of the Brachyura, for example, Brösing et al. (2001) investigated the characteristics of the cardiac foregut ossicles and proposed a new phylogeny for this group based on this character. Felgenhauer and Abele (1989) have suggested that the basic structure of the foregut in the lower Decapoda is closely related to phylogeny, although details of the structures may be related to diet.

This paper elucidates the morphology of the cardiac and

pyloric foreguts of *Aegla platensis* Schmitt, 1942, a species widely distributed in the freshwater systems of Uruguay, Argentina and southern Brazil.

Materials and methods

We examined 80 specimens of *Aegla platensis* collected in the River Gravataí drainage-basin (29°46′S, 50°53′W) in the southern Brazilian state of Rio Grande do Sul (RGS), along with other specimens selected from the crustacean collection of the Zoology Department of the Federal University of RGS (UFRGS). Foreguts were dissected and fixed in buffered 10% formalin, and dorsal, ventral and para-sagittal cuts made. Foreguts were prepared for scanning electron microscopy as described by Felgenhauer (1987), using a model CPD 030 critical point dryer (BAL-TEC) with subsequent gold-coating, and later, the photomicroscopy being carried out in a JEOL JSM 580 scanning electron microscope (15 and 20 KV) at the Electron Microscopy Center, UFRGS. Ossicles were described and identified based on the nomenclature of Ngoc-Ho (1984) and Kunze and Anderson (1979).

Results

The cardiac foregut ossicles include the gastric mill, lateral wall and cardiac-pyloric valve ossicles (Table 1), together with the dorsal, ventral and lateral ossicles of pyloric region.

Table 1. Ossicles of the foregut of Aegla platensis.

Ossicle	Paired	Unpaired	Tooth
Gastric Mill			
Mesocardiac		X	
Pterocardiac	X		
Urocardiac		×	X
Zygocardiac	X		×
Pyloric		×	
Propyloric		X	X
Exopyloric	X		
Lateral Cardiac			
Pectineal	X		X
Prepectineal	X		
Postpectineal	X X X		
Inferior lateral cardiac	X		
Subdentate	X		
Cardiopyloric Valve			
Anterior of cardiopyloric valve		X	
Dorsal Pyloric			
Posterior mesopyloric		X	
Uropyloric		×	
Ventral Pyloric			
Anterior inferior pyloric		×	
Middle inferior pyloric		X	
Posterior inferior pyloric	X		
Transverse pyloric		X	
Lateral Pyloric			
Anterior pleuropyloric	X		
Middle pleuropyloric	X		
Posterior pleuropyloric	×		

The foregut of Aegla platensis presents two well-defined regions: the cardiac foregut at the anterior end and the pyloric foregut at the posterior end (Fig. 1). The cardiac foregut (region A in Fig. 1) is guarded at the entrance by a pair of oesophageal valves (Fig. 8, ve), and consists of a large triangular chamber, supported by thin calcified plates, and by a set of very thick calcified ossicles. The central urocardiac ossicle bears the median tooth (Fig. 5), and is articulated to the large central mesocardiac ossicle anteriorly, and to the propyloric ossicle posteriorly (Fig. 1). The mesocardiac ossicle articulates with the paired pterocardiac ossicles laterally, and these ossicles, to the paired zygocardiac ossicles, which bear the lateral teeth (Fig. 6), being responsible for mastication and triturating of food entering from the oesophagus. The paired pectineal ossicles of the lateral wall bear the accessory teeth (Fig. 7), which assist in pushing material into the central region of the foregut. This elaborate apparatus of trituration, composed by the median tooth of urocardiac ossicle, lateral teeth of zigocardiac ossicles, and accessory teeth of the pectineal ossicles, is highly calcified and is often called "gastric mill". A peculiarity of the zigocardiac ossicles is the occurrence of a series of spines at their anterior margin (Fig. 6, zs), structures not so far recorded in the literature for any other decapod. The remaining ossicles of the cardiac foregut, serve to support the foregut chamber in the same way as the ossicles and chitinous plates of the lateral walls do, for example, the paired inferior lateral cardiac and the postpectineal ossicles (Fig. 8) and the cardio-pyloric valve. In the

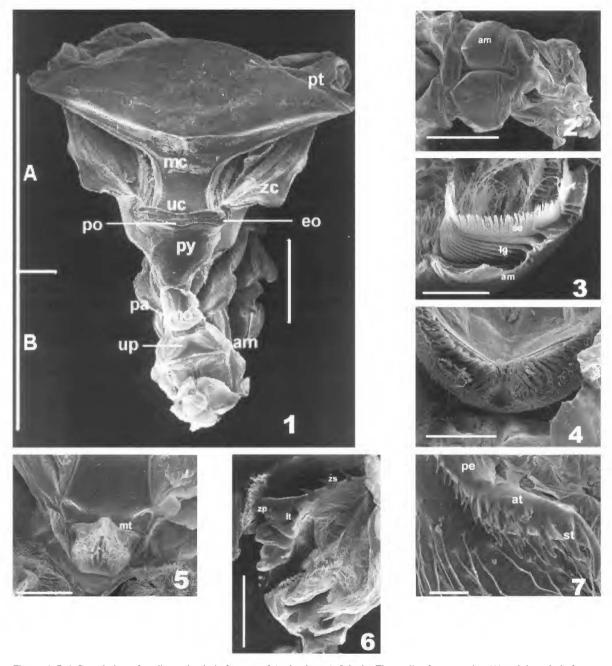
analysed foreguts it was possible to see that some ossicles of lateral wall were fused (e.g. the prepectineal were fused with the pectineal). On the other hand, ossicles such as the inferior cardiac, posterior-lateral cardiac, supra-ampullar, mesopyloric posterior and the lateral ossicles of the cardio-pyloric valve were not observed in A. platensis. The pyloric foregut is a smaller chamber, posterior to the cardiac foregut (region B in Fig. 1), and is made up of various ossicles, valves, grooves, ridges, channels and two rounded ampullae, all of which constitute the filtering mechanism of the foregut. The pyloric foregut is internally divided into dorsal and ventral regions, shown in Fig. 2, with the dorsal region possessing a central channel and the pleuropyloric valve (Fig. 8) which allows the passage of large particles into the intestine and acts in the production of the faecal pellets. The ventral region is characterised by two ampullae (Figures 2 and 3), which constitute the most important structure of this part of the foregut, carrying out the filtering of the food particles by the setae, and which are externally characterised by two calcified semi-circular plates. The interior of the pyloric ampullae is divided into two chambers, the superior chamber containing the filter-press and the inferior chamber (Fig. 3) containing parallel longitudinal grooves. The filter-press adjusts to the concave shape of the inferior chamber, compressing food particles against the parallel grooves, and then trapping larger particles within a series of setae (Fig. 3).

The cardiac and pyloric foreguts are separated by the cardiac-pyloric valve (Fig. 4), a structure which regulates the passage of triturated food particles from the gastric mill to the pyloric foregut where they are further filtered.

Discussion

The general morphology of the cardiac and pyloric foreguts of *A. platensis* is similar to that described by Icely and Nott (1992) for decapods in the infraorders Astacidea, Thalassinidea, Palinura, Anomura and Brachyura. The basic structure of the decapod foregut is confirmed for the *A. platensis* foregut in this work, although there are differences which probably reflect the type of food that is being treated in the foregut.

Compared with the diogenid anomurans Clibanarius taeniatus, C. virescens, Paguristes squamosus and Dardanus setifer (Kunze and Anderson, 1979), the cardiac foregut structures of A. platensis are well-developed, with this last species presenting a complex cardiac foregut equipped with specialised mechanisms for the trituration of food. These specialised mechanisms can be seen in the robust and ornamented medial (Fig. 5) and lateral (Fig. 6) teeth, as well as the accessory teeth (Fig. 7) which are elongate with a greater number of spines, when compared with the diogenids studied by Kunze and Anderson (1979). On the other hand, the spines observed at the anterior margin of the zigocardiac ossicles problably increases the capacity of triturating food particles. This complex form of foregut can be associated with macrophagy and predation in which large particles are ingested (Dall and Mortiary, 1983). Macrophagy and predation are well characterised in A. platensis, an omnivorous species feeding on aquatic insect larvae and



Figures 1–7. 1. Dorsal view of cardiac and pyloric foreguts of *Aegla platensis* Schmitt. The cardiac foregut region (A) and the pyloric foregut region (B) are indicated by lines. Abbreviations: am, pyloric ampullae; eo, exopyloric ossicle; mc, mesocardiac ossicle; mo, mesopyloric posterior ossicle; pa, anterior pleuropyloric ossicle; py, pyloric ossicle; po, propyloric ossicle; pt, pterocardiac ossicle; uc, urocardiac ossicle; up, uropyloric ossicle; zc, zygocardiac ossicle (scale bar: 1mm). 2. Ampullae of pyloric foregut. Abbreviation: am, pyloric ampullae (scale bar: 1mm). 3. Internal view of the inferior chamber of the ampullae. Abbreviations: am, pyloric ampullae; lg, longitudinal parallel grooves; se, setae (scale bar: 0.15mm). 4. Cardiopyloric valve (scale bar: 0.5mm). 5. Median tooth of the urocardiac ossicle. Abbreviation: mt, median tooth (scale bar: 0.5mm). 6. Zygocardiac ossicle with the lateral teeth and spines. Abbreviations: lt, lateral teeth; zs, zygocardiac spines; zp, zygocardiac molar processes (scale bar: 1mm). 7. Accessory teeth of the pectineal ossicle. Abbreviations: at, accessory teeth spines; pe, pectineal ossicle (scale bar: 0.15 mm).

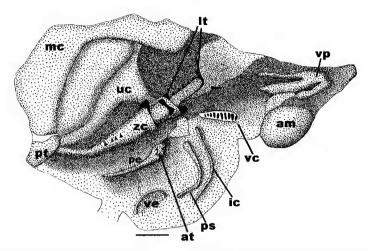


Figure 8. Sagittal half of the foregut showing internal organisation. Abbreviations: am, pyloric ampullae; at, accessory teeth; ic, inferior lateral cardiac ossicle; It, lateral teeth; mc, mesocardiac ossicle; pe, pectineal ossicle; ps, postpectineal ossicle; pt, pterocardiac ossicle; uc, urocardiac ossicle; vc, cardiopyloric valve; ve, esophageal valve; vp, pleuropyloric valve; zc, zygocardiac ossicle (scale bar: 0.65mm).

macrophytes (Bueno and Bond-Buckup, 2001). The differences between the foreguts of the aeglids and diogenids in terms of the specialisation of the gastric mill may reflect different feeding habits of these species, as was suggested by Kunze and Anderson (1979) for the diogenid species. The variation between foreguts is more marked when considering the cardiac foregut ossicles, which may be fused or absent (Meiss and Norman, 1977) Inversely, the inferior cardiac, posterior-lateral cardiac, supra-ampular, mesopyloric posterior and the lateral ossicles of the cardio-pyloric valve have been observed in other anomurans, Clibanarius taeniatus, C. virescens, Paguristes squamosus and Dardanus setifer (Kunze and Anderson, 1979) and Galathea squamifera (Ngoc-Ho, 1984). It is possible that the ossicles not seen in A. platensis were indeed present but their identification was not possible because they were strongly fused with other ossicles.

The basic organisation of the cardiac ossicles of *A. platensis* follows the same arrangement found in the majority of decapods, all of which (except for some Caridea) present an elaborate food trituration mechanism — the gastric mill (McLaughlin, 1983; Growns and Richardson, 1990).

Meiss and Norman (1977), stated that decapod infraorders with species which have more complex gastric mills (e.g. Brachyura and paguroid Anomura) have a smaller mesocardiac ossicle, a well developed pyloric ossicle and large urocardiac and zygocardiac ossicles. The structural complexity of the cardiac foregut of *A. platensis*, observed in our sample, supports this hypothesis.

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